

Geographic Variation in Natural Populations of *Speyeria callippe* (Boisduval) (Lepidoptera: Nymphalidae)

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Abstract.—The geographic variation in 8 wing characters in 35 populations of *Speyeria callippe* (Boisduval) is described and the covariation of the characters summarized. Univariate (SS-STP), discriminant function, and principal components analyses were performed to describe the variation, interpret its origins, and group together geographically adjacent localities that are similar in their characteristics. These techniques are used to test the ability of characters to differentiate subspecies. All three techniques corroborate that these characters, which have previously been used to differentiate 16 subspecies, cannot do so with any statistical significance. Thus, the subspecific taxonomy of *S. callippe* is revised. The presently recognized 16 subspecies are reduced to 3, whose morphological features correlate with their geographic distributions.

The subspecies concept and its utility have been critically evaluated by numerous systematists (Bohme, 1978; Mayr, 1969; Wilson and Brown, 1953), yet many problems remain in defining and naming subspecies. At issue is a growing discontent with an arbitrary taxonomic category, the subspecies, which often fails to accurately describe infraspecific variation. In certain animal groups, such as butterflies, where the ratio of systematists to species is high, minor differences in morphology are accorded relatively high value in determination of taxonomic rank. Mayr (1969) defined the subspecies as “an aggregate of local populations of a species, inhabiting a geographic subdivision of the range of the species, and differing taxonomically from other populations of the species.” Clearly the determination of how distinctive geographical segregates of a species must be to warrant formal taxonomic recognition is an arduous task. Most butterfly subspecies are named on the basis of one or a few wing characters, principally slight differences in color, maculation pattern, or size. Generally these differences are intuitively perceived by a worker, rather than supported by statistical analyses of character variation throughout the geographic range of the species.

This study describes the geographic variation in 8 wing characters of *S. callippe*. Characters that have previously been used to differentiate subspecies are analyzed as well as others to discover which are most useful for defining patterns of variation that relate to geographic distribution of the butterflies. Hovanitz (1941, 1943), Howe (1975), Moeck (1957), and Sette (1962) speculated that the variation in several characters, including size, wing color, and silver-spot patterns, of the numerous subspecies of *Speyeria callippe* was clinal. Also they proposed that the pattern of variation in several characters partitioned populations into several geographical segregates or subspecies. Despite the large degree of overlap in the



Figure 1. Geographic distribution of the formerly recognized subspecific taxa of *Speyeria callippe*. Taxa in large capital letters, with a Great Basin distribution, are green-disced populations, whereas those represented by the smaller lower-case letters, with a California-Oregon distribution, are brown-disced populations.

range of variation of numerous wing characters, 16 subspecies are currently recognized (dos Passos, 1964; Miller and Brown, 1981).

Several univariate and multivariate numerical taxonomic techniques were used to analyze the geographic variation in 35 populations scattered throughout the range of *S. callippe*. Based on these analyses and other numerical taxonomic studies (Arnold, 1983, 1985) new conclusions about phenotypic character vari-

ation and the infraspecific nomenclature of *Speyeria callippe* are presented. The presently recognized 16 subspecies (Fig. 1) are reduced to three whose morphological features correlate with geography.

DATA COLLECTION AND ANALYSIS

Materials.—Initially, 35 populations or operational taxonomic units (OTU's), were selected for this study (Table 1). Samples of 10 males from each population were chosen by use of a random numbers table. Each sample was composed of individuals collected on the same date at the same locality. The subspecific identity (*sensu* dos Passos, 1964) of each sample was determined. Nineteen additional populations were later used as unknowns to test the effectiveness of the characters under analysis in distinguishing subspecific taxa.

Table 1. List of 35 *Speyeria callippe* populations (OTU's) analyzed using univariate and multivariate statistical techniques. OTU's associated with two subspecific names (e.g., OTU number 2 *comstocki*: *callippe*), indicate that these are intermediate populations.

OTU	OTU no.	Former subspecific identity	Locality data
CALC	1	<i>comstocki</i>	San Diego Co., CA
CHEW	2	<i>comstocki</i> : <i>callippe</i>	Chew's Ridge, Monterey Co., CA
MOCH	3	<i>callippe</i> : <i>comstocki</i>	Arroyo Mocho, Alameda Co., CA
MILL	4	near <i>callippe</i>	Oakland, Alameda Co., CA
LIVE	5	<i>callippe</i> : <i>comstocki</i>	Los Mochos Cyn., Alameda Co., CA
NCAL	6	<i>callippe</i> : <i>comstocki</i>	Del Puerto Cyn., Stanislaus Co., CA
CALL	7	<i>callippe</i>	San Bruno Mtn., San Mateo Co., CA
NAPA	8	<i>liliana</i>	Mt. Veeder, Napa Co., CA
LCAL	9	<i>liliana</i>	Boggs Mtn., Lake Co., CA
LRCA	10	<i>liliana</i> : <i>rupestris</i>	Eel River, Mendocino Co., CA
GLEN	11	<i>liliana</i>	Mendocino Pass, Glenn Co., CA
MEND	12	<i>liliana</i>	Mendocino Pass, Glenn Co., CA
RCAL	13	<i>rupestris</i>	Shasta-Trinity Co. line, CA
TRIN	14	<i>elaine</i> : <i>rupestris</i>	Mt. Shasta, Siskiyou Co., CA
ECAL	15	<i>elaine</i>	Siskiyou Summit, Jackson Co., OR
CALS	16	<i>sierra</i>	Red Clover Valley, Plumas Co., CA
PLUM	17	<i>sierra</i> : <i>juba</i>	Feather River, Plumas Co., CA
BUTT	18	<i>juba</i>	Big Battle Creek, Butte Co., CA
FIDD	19	<i>juba</i>	10 mi. E. Fiddletton, Amador Co., CA
ICAL	20	<i>juba</i>	10 mi. E. Fiddletton, Amador Co., CA
PION	21	<i>laura</i>	Washoe Co., NV
ALPI	22	<i>nevadensis</i>	Monitor Pass, Alpine Co., CA
MLCA	23	<i>laurina</i>	Tulare Co., CA
LAUR	24	<i>laurina</i>	Tulare Co., CA
MCAL	25	<i>macaria</i>	Glenville, Kern Co., CA
GREE	26	<i>macaria</i> : <i>laurina</i>	Tehachapi Mtns., Kern Co., CA
TEHA	27	<i>macaria</i>	Tehachapi Mtns., Kern Co., CA
SCAL	28	<i>semivirida</i>	Harney Co., OR
NEVA	29	<i>nevadensis</i>	several counties, NV
HARM	30	<i>harmonia</i>	several counties, UT
CALG	31	<i>calgariana</i>	Calgary, Alberta, Canada
MEAD	32	<i>meadii</i>	several counties, CO
UTAH	33	<i>harmonia</i>	several counties, UT
GALL	34	<i>gallatini</i>	several counties, WY
GUNN	35	<i>meadii</i>	Boulder Co., CO

Table 2. Characters used in univariate, discriminant function and principal component analyses. Character types are continuous (C) and nonordered (NO) multi-state. Non-correlated characters that were used in the numerical taxonomic analyses are denoted by a *.

Character	Name	Type	Veins measured or states
*1) FWLE	forewing length	C	base of R to distal end of M1
2) FWWD	forewing width	C	R4 to 2A at distal margin
*3) FWLW	ratio of forewing length/width	C	ratio of FWLE/FWWD
4) FDCL	forewing discal cell length	C	base of M to its junction with M1
5) FDCW	forewing discal cell width	C	M1 to M3 at distal end of cell
*6) FDLW	ratio of forewing discal cell length/width	C	ratio of FDCL/FDCW
7) HWLE	hindwing length	C	base of M to distal end of M1
8) HWWD	hindwing width	C	Rs to 2A at distal margin
*9) HWLW	ratio of hindwing length/width	C	ratio of HWLE/HWWD
*10) HDCL	hindwing discal cell length	C	base of M to its junction with M1
11) HDCW	hindwing discal cell width	C	M1 to M3 at distal margin
12) HDLW	ratio of hindwing discal cell length/width	C	ratio of HDCL/HCDW
*13) DISC	disc color of hindwing venter	NO	green, brown, or green and brown
*14) SUHW	silver spot pattern on hindwing	NO	none, only near body, only distal, or entire wing
*15) USGC	ground color of dorsal facies	NO	pale yellow, yellow, orange, or reddish-orange

Characters.—Twelve quantitative (continuous) and 3 qualitative (non-ordered) wing characters (Table 2) were measured for each of the 350 individuals. Scores for the 10 males in each population were averaged to derive a population score for each character. Continuous characters were measured along specified veins with dial calipers to the nearest 0.1 mm. These characters were selected based on their ease of measurement. Overall size has been previously used to delimit some of the subspecies (Howe, 1975; dos Passos and Grey, 1947), thus the continuous characters were analyzed in an attempt to define the range of size variation in each subspecies. Length and width raw data were transformed logarithmically to standardize the data prior to analysis. Thus each character contributes toward the overall resemblance inversely in proportion to its variability among the entire set of OTU's. Characters with a small range of variation contribute equally as characters with a large range of variation. The characters described by ratios were, by definition (Clifford and Stephenson, 1975), transformed. A histogram for each continuous character was plotted to verify that its distribution was normal. For the three non-ordered characters, each specimen was compared to a series of standards representing each character state. Pearson product-moment correlation coefficients were calculated for each pair of characters to determine the extent

each character imparts unique information as opposed to information in common with the other characters being analyzed.

Data analysis.—The approach used to analyze geographic variation in the morphological characters was as follows:

- 1) partitioning of the variation of each character by analysis of variance (univariate or SS-STP analysis);
- 2) correlation of characters in order to represent the variation in them by a smaller number of factors (principal components analysis);
- 3) simultaneous comparison of the variation in all characters to portray the similarities between populations and assess the degree of geographic segregation of similar populations (discriminant function analysis);
- 4) test the ability of the characters used to differentiate the 16 subspecies and determine the best subspecific classification.

RESULTS

Character correlations.—Mean character states for each population were used to compute the correlation coefficient between every pair of the 15 characters originally measured. The correlation between characters measures the similarity (concordance) of their patterns of geographic variation. Seven of the characters were highly correlated with one or more other characters (>0.70). These were eliminated from further numerical taxonomic analyses. Thus the geographic variation in 8 uncorrelated or weakly correlated characters, FWLE, FWLW, FDLW, HWLW, HDCL, DISC, USGC, and SUHW, was analyzed (Table 2).

Univariate analysis.—The recognition of 16 subspecies (dos Passos, 1964) and previous analyses of infraspecific variation (Hovanitz, 1941, 1943) suggest that the character variation is discontinuous and that the range of *callippe* can be divided into different homogeneous regions. This categorization can be tested by using multiple comparison techniques (Sokal and Rohlf, 1969).

In order to ascertain which characters could partition the 35 populations into statistically significant subsets, analysis of variance over all localities was performed for each of the 8 morphometric characters using Power's (1970) version of Gabriel's (1964) simultaneous test procedure (SS-STP), a multiple comparison test between means (Gabriel and Sokal, 1969). This procedure calculates character means of populations, ranks the means for each character, and computes homogeneous subsets of means based on the variances. Computations were made using the computer program UNIVAR (Moss, 1969).

Population means were plotted for each character to examine patterns of variation. Following the technique of Doyen (1973), shaded circles appear to the left of the ranked means on the accompanying distribution maps (Figs. 2–9). These circles do not correlate with the overlapping subsets of the STP technique, but to a second grouping of the means based on dividing the total range of ranked means for each character into 5 equal intervals. Largest values are represented by open circles, and smallest values by closed circles.

Only one character, ventral disc color (DISC) exhibited variation concordant with geography. All brown OTU's (depicted by open circles in Fig. 9) occur from the Sierra Nevada Mountain range to the west coast, while all green populations (black circles) are located in the Great Basin and Rocky Mtns. (Fig. 9). The green-brown intermediates (half open-half black circles) are from southern Oregon, an

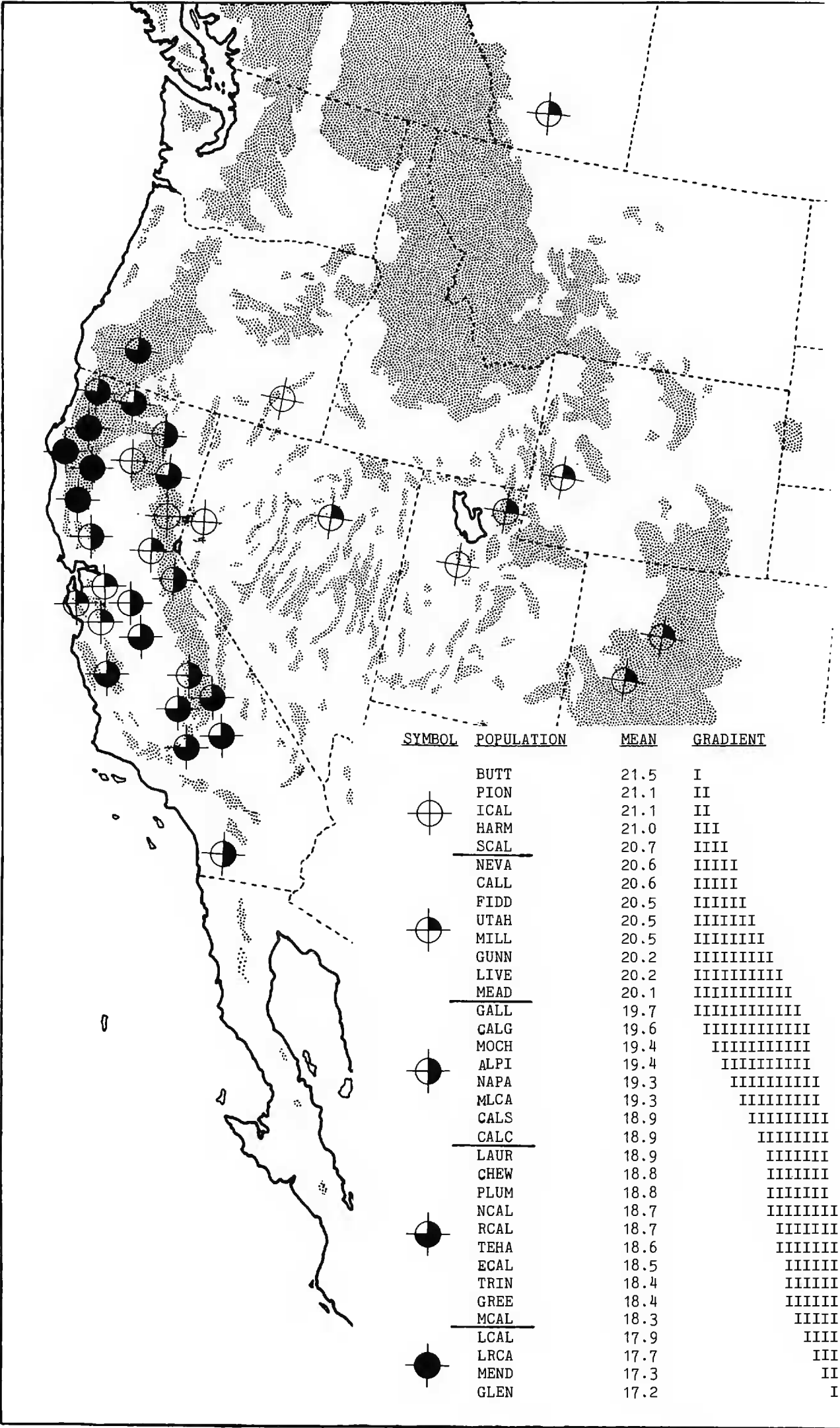


Figure 2. Results of univariate (SS-STP) analysis for character FWLE. The circles are used to check for clinal variation in FWLE, after the technique of Doyen (1973).

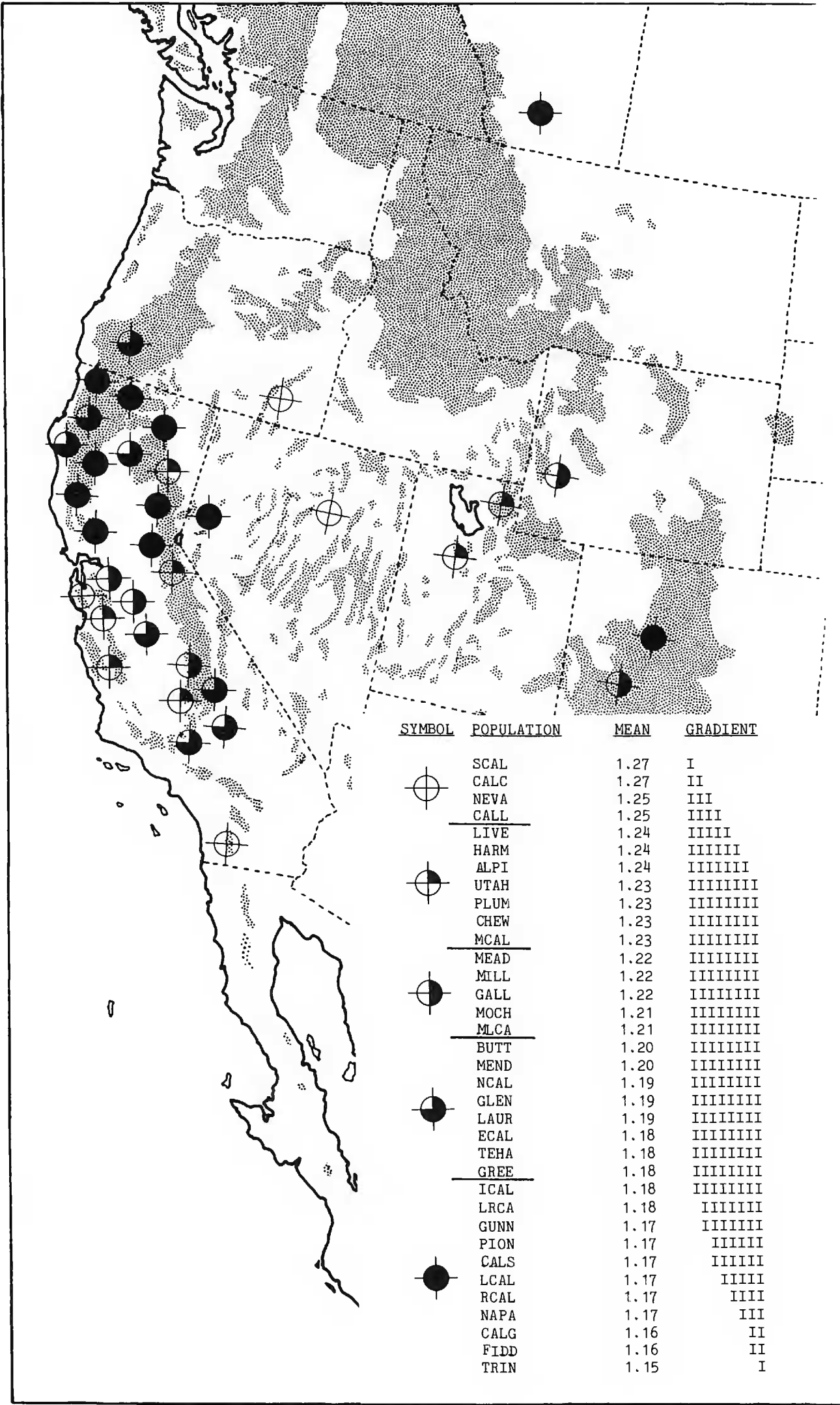


Figure 3. Results of univariate (SS-STP) analysis for character FWLW. The circles are used to check for clinal variation in FWLW, after the technique of Doyen (1973).

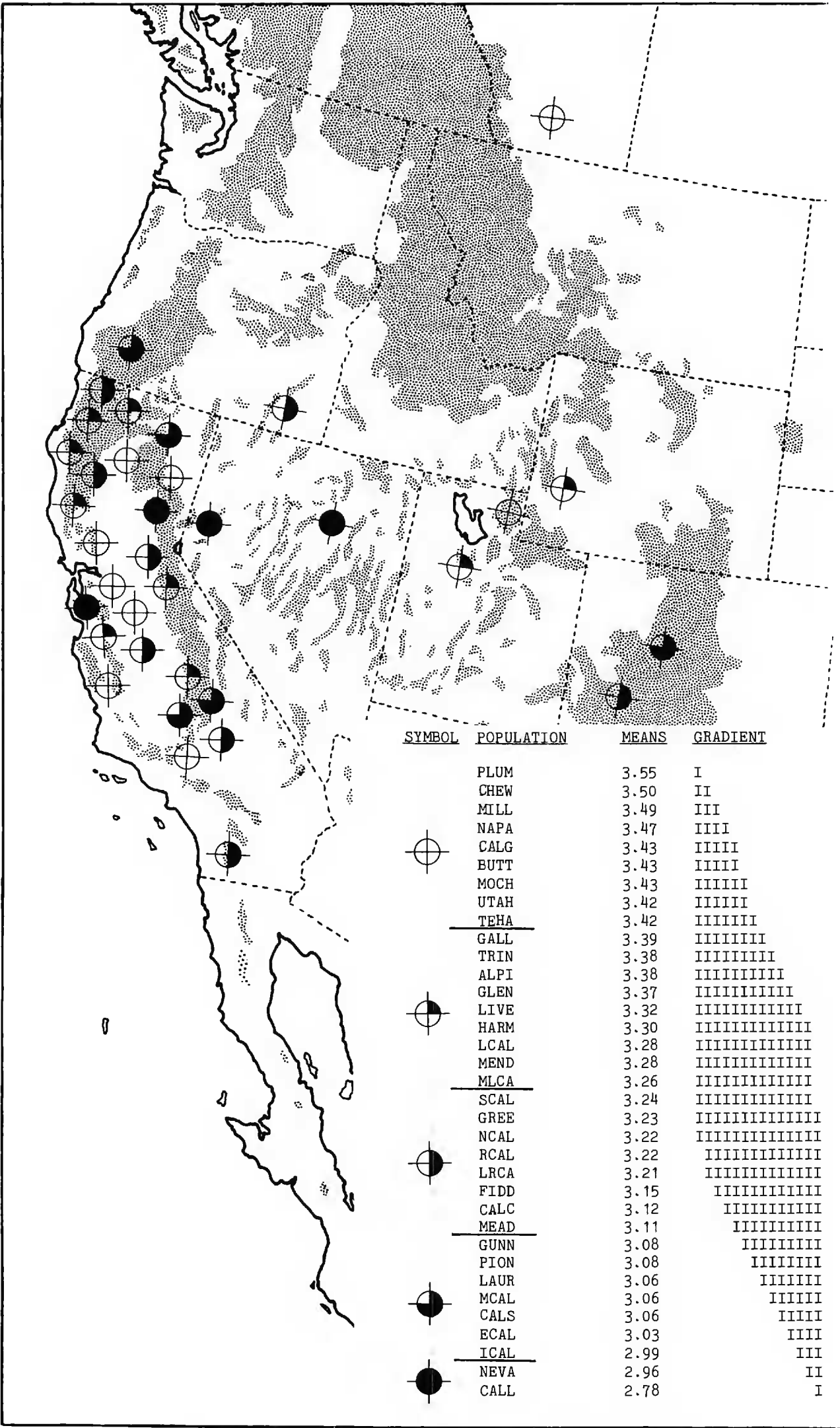


Figure 4. Results of univariate (SS-STP) analysis for character FDLW. The circles are used to check for clinal variation in FDLW, after the technique of Doyen (1973).

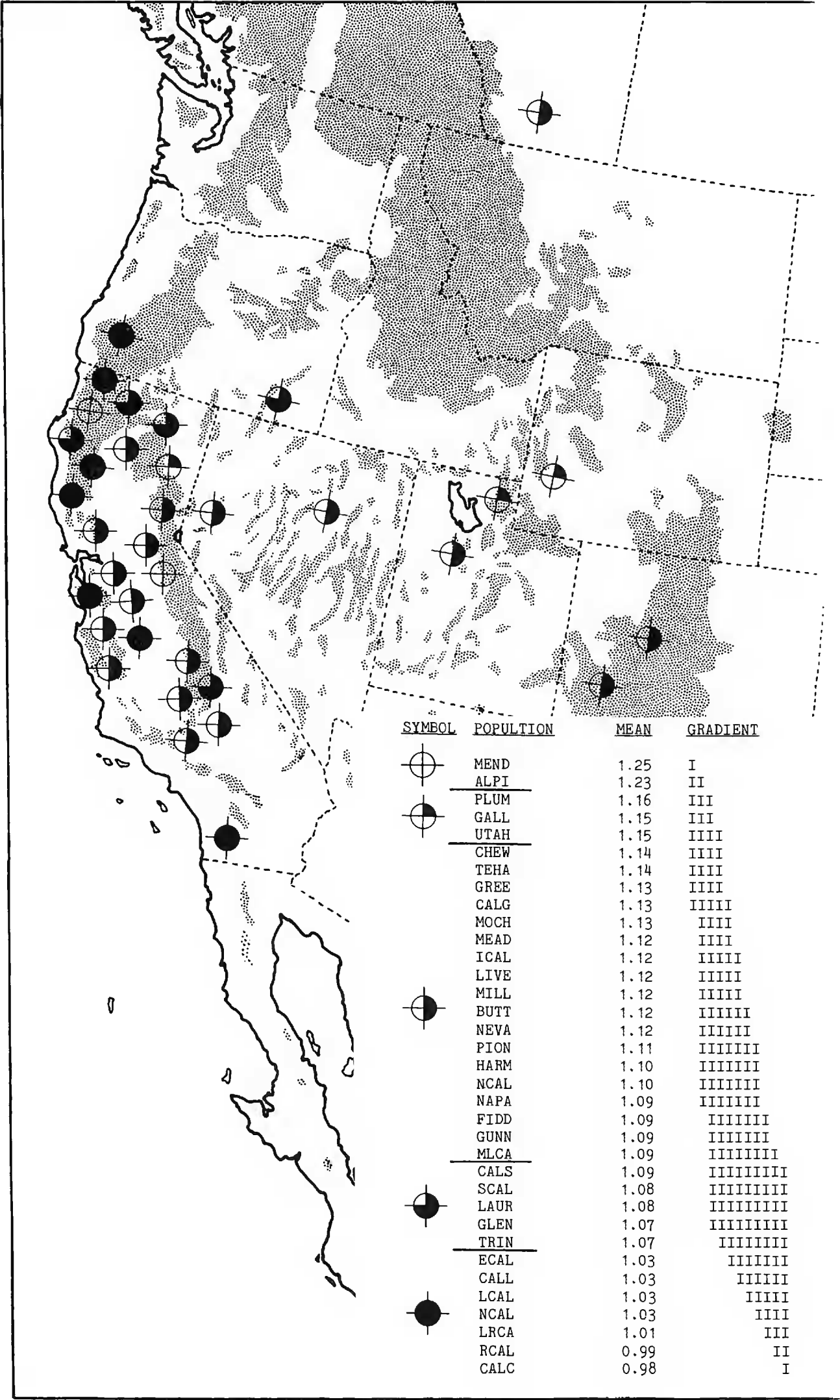


Figure 5. Results of the univariate (SS-STP) analysis for character HWLW. The circles are used to check for clinal variation in HWLW, after the technique of Doyen (1973).

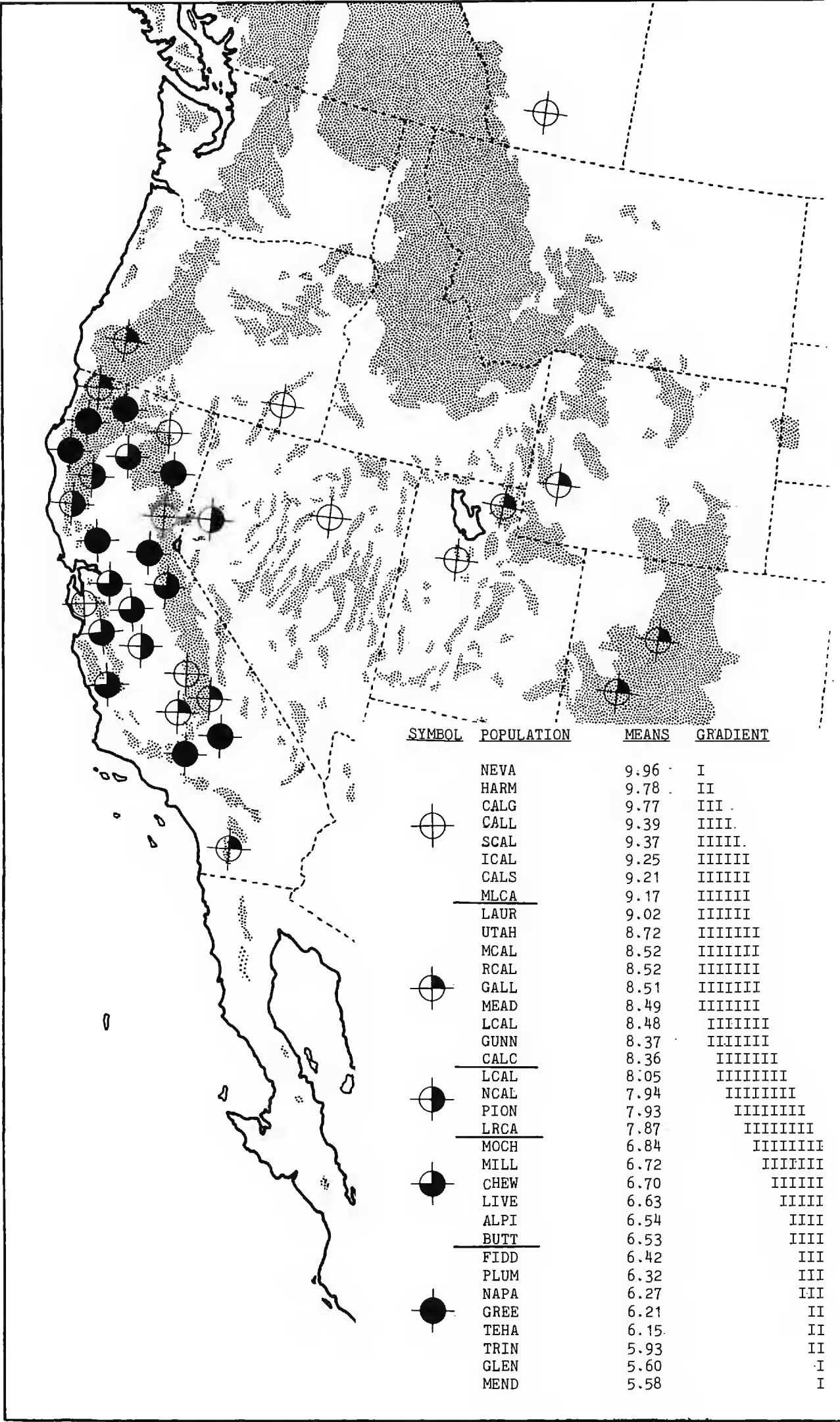


Figure 6. Results of the univariate (SS-STP) analysis for character HDCL. The circles are used to check for clinal variation in HDCL, after the technique of Doyen (1973).

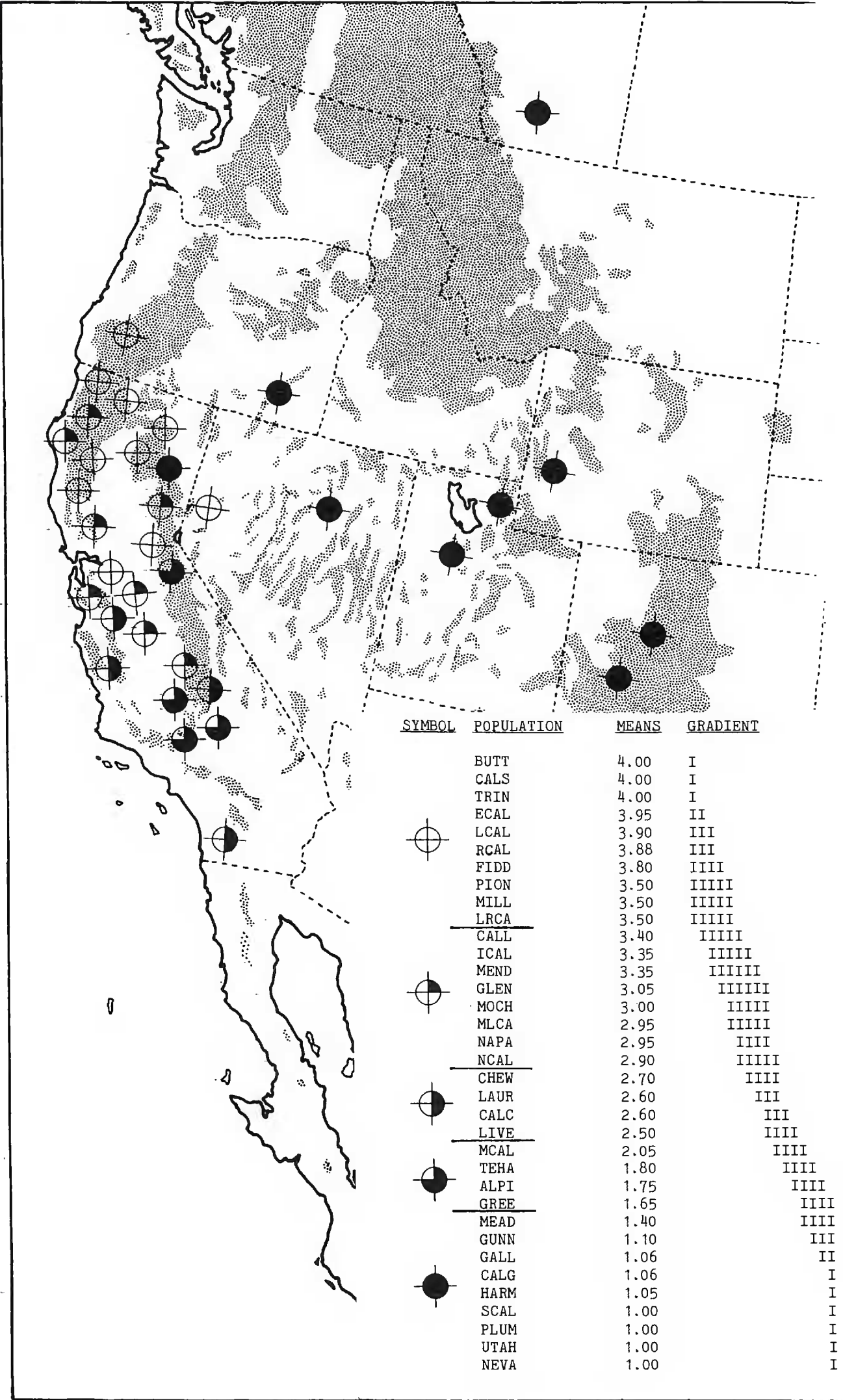


Figure 7. Results of the univariate (SS-STP) analysis for character USGC. The circles are used to check for clinal variation in USGC, after the technique of Doyen (1973).

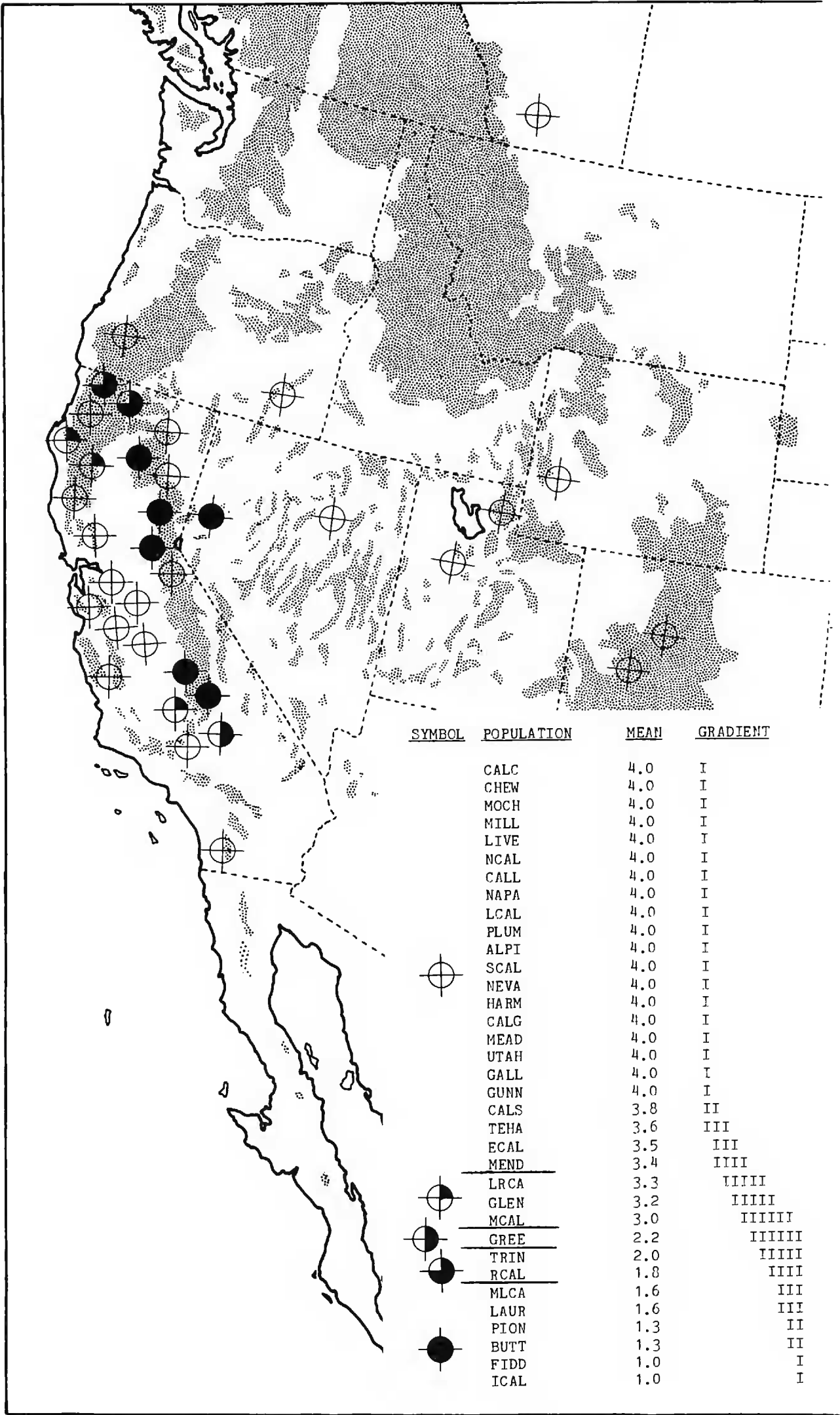


Figure 8. Results of the univariate (SS-STP) analysis for character SUHW. The circles are used to check for clinal variation in SUHW, after the technique of Doyen (1973).

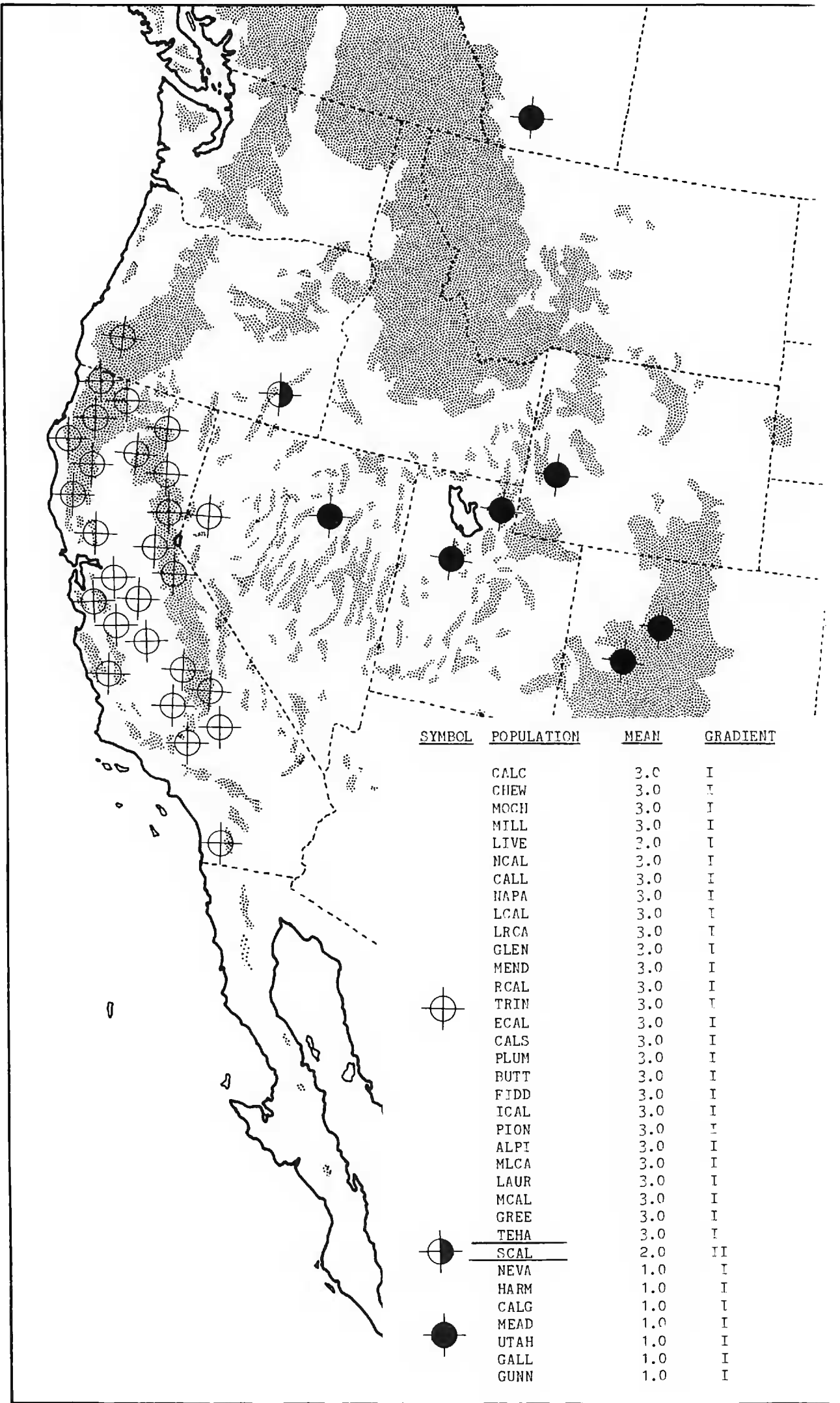


Figure 9. Results of the univariate (SS-STP) analysis for character DISC. The circles are used to check for clinal variation in DISC, after the technique of Doyen (1973).

area where Great Basin and Cascade populations may naturally come into contact. Discordant variation was noted for the remaining 7 characters (Figs. 2–8), each of which was characterized by abrupt discontinuities. Only one character, FWLE (Fig. 2), offered a hint of localized clinal variation. The SS-STP subsets of the other 7 characters included considerable overlap of green and brown populations.

Discriminant function analyses.—With this technique, measurements of two or more characters are weighed and combined linearly to provide maximal separation for two or more groups. Each analysis begins with groups of known identity, in this case the 16 subspecies *sensu* dos Passos (1964) and Miller and Brown (1981). This multivariate method uses the non-overlapping information contributed by each character to produce a linear function that will classify the known specimens with a minimum probability of misidentification. Different combinations of characters may be used to achieve statistical distinction between groups. These procedures assist in determining which characters most effectively partition the OTU's into groups.

Direct and step-wise discriminant function analyses were performed on the same data matrix using the Mahalanobis generalized distance, D^2 (Klecka, 1975), to measure phenetic similarity of groups. The 8 characters were first analyzed using the direct method, where all variables are simultaneously entered into the analysis. Discriminant analysis defines axes through the multi-dimensional clusters of individuals resulting in the maximum separation of the clusters.

Later, a step-wise analysis was performed, in which characters were added or removed from the discriminant function analysis based on their contribution to the total distance among multivariate means. This criterion is measured by their F-values, a statistical indication of the relative importance of each character. Characters having the largest F-values are repeatedly selected for partitioning groups of individuals (i.e., clusters) as they contribute more to the classification process. Each step adds the character with the next highest F-value to yield the greatest separation of clusters. Thus the step-wise procedure indicates a character's importance in separating groups, and the least number of characters necessary to separate the clusters.

Both analyses revealed that ventral disc color (DISC), a non-parametric character, had the greatest power of separation based on the F-values for each of the 8 characters (Table 3). DISC could separate all green populations from all brown populations, but could not significantly separate any subsets within the green or brown populations. According to the F-values (Table 3), the next most powerful separation was based upon a parametric character, HDCL, but it could not separate the populations into meaningful clusters. DISC was the only character which could significantly separate local populations.

Linear discriminant function analysis also provides an objective means by which unknown populations can be classified based on the analyses of the reference groups. The scores for individuals from each group form distributions, each with a mean score. The midpoint between mean scores is used to determine group membership, because this point gives the minimum misclassification. Unless the separation of known groups is complete, scores for some specimens will fall within the range of scores delimiting another population, and these individuals would be misclassified. The rate of misclassification of known specimens provides a measure to the effectiveness of a set of characters in identifying new specimens.

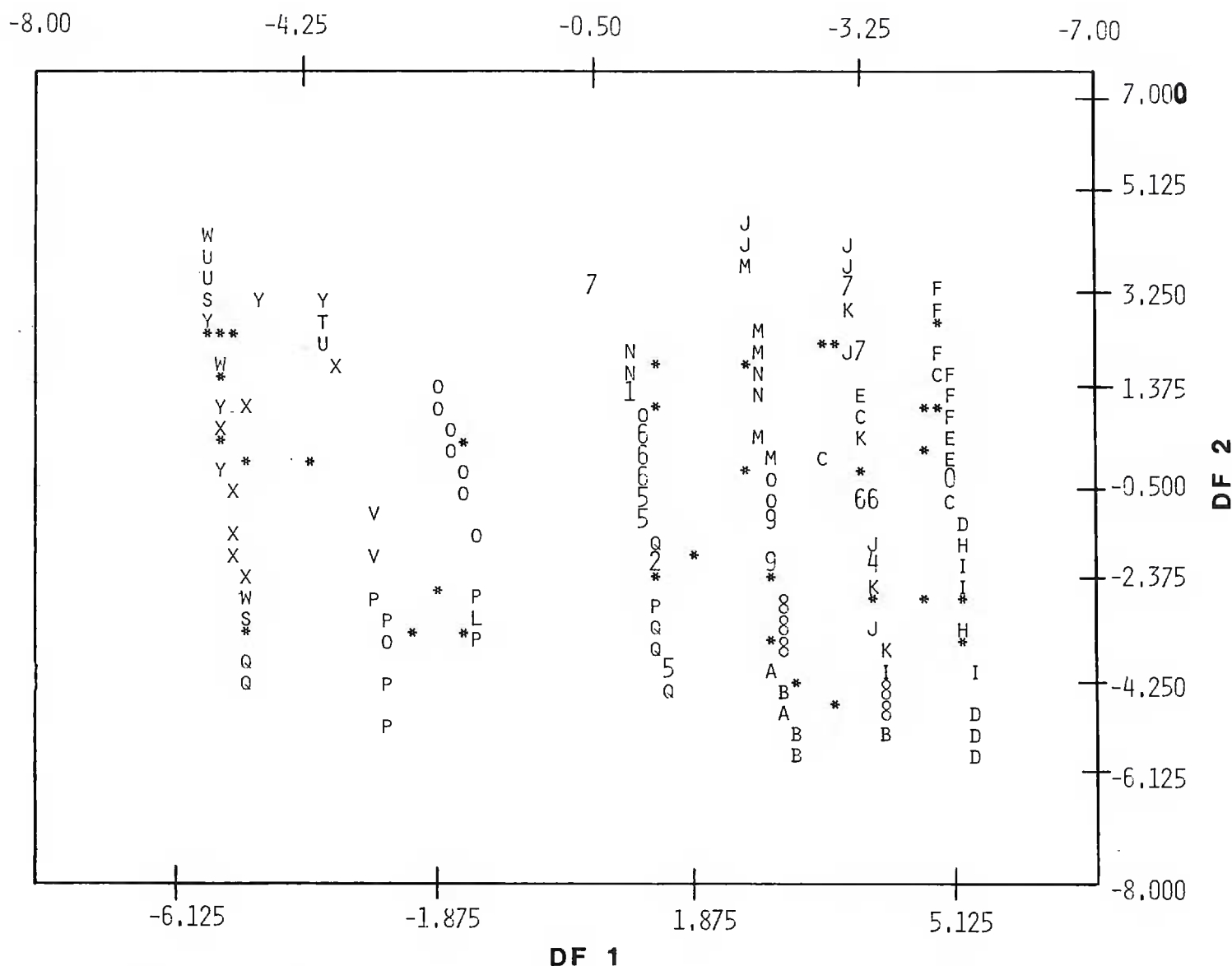


Figure 10. Territorial map of individuals in the 35 *Speyeria callippe* populations (represented by letters A–Z and numbers 0–9) based upon discriminant function scores 1 and 2 (axes are labelled DF 1 and DF 2). Centroids of the 35 populations are indicated by stars. Note the extensive amount of overlap by individuals of different populations.

The classification routine correctly identified only 82 of 190 unknowns (43.2%) as members of the local populations to which they actually belong. As a double check, the 350 individuals which composed the reference populations were then run as unknowns. Only 161/350 (46.0%) of the individuals were correctly classified. Thus most individuals were classified as having their highest group probability as members of populations other than that to which they actually belong. The territorial map of discriminant score 1 vs. score 2 illustrates this degree of overlap among populations (Fig. 10).

In order to remove any bias introduced into the discriminant functions due to the three non-parametric (qualitative) characters, a third analysis using only the 5 continuous characters to partition OTU's was performed. During the classification routine only 60/190 unknowns (31.6%) and 119/350 (34.0%) reference individuals were correctly classified. This strongly suggests that overall size is a poor character for distinguishing subspecies of *S. callippe*.

Principal components analysis (PCA).—The prior assignment of populations into arbitrary reference groups is not necessary with this technique. Combinations of character axes (eigenvectors) representing OTU's are transformed to uncorre-

Table 3. Ranking of characters based on their ability to partition populations (OTU's) as determined by step-wise discriminant function analysis. Higher F-values indicate characters which best discriminate between groups.

Character	F to enter or remove
13) DISC	129.9
10) HDCL	35.9
15) USGC	24.6
1) FWLE	7.9
9) HWLW	1.2
3) FWLW	1.1
14) SUHW	1.0
6) FDLW	0.9

lated axes represented in an n-dimensional character hyperspace. The first component accounts for the greatest percentage of variation, the second accounts for the next greatest percentage of variation, etc., until all variation among all OTU's is expressed. Thus, the spatial relationships between OTU's in the n-dimensional character space are preserved while the axes are rotated. If a major proportion of the variability between characters is explained by the first 3 eigenvectors, the OTU's can be represented in 3-dimensions without much distortion to their real relationships. Factor loadings for all characters on each component provide a basis for inferring which characters are discriminatory and which are uncorrelated.

The first three principal components accounted for 83.2% of the variance observed (Table 4). Factor loadings for the three non-ordered state characters are all near zero along the first and second principal components. This indicates that the qualitative characters contribute little to the character variation along these components. In contrast, the five continuous characters exhibit higher loadings along the first and second components. The relative homogeneity of eigenvalues suggest that the continuous characters along these principal components reflect general size factors for the OTU's.

Continuous characters along the third component have low loadings, while the non-ordered state characters exhibit higher loadings. This indicates that the non-ordered characters are instrumental in explaining the variation along this component. Continuous characters express differences due to size, while the non-

Table 4. Factor loadings (i.e., eigenvalues) as determined by the principal components analysis. Factors with the highest eigenvalues explain most of the observed variance.

Factor	Eigenvalue	Percent of variance	Cumulative percentage
1	6.05	43.2	43.2
2	3.09	23.0	66.2
3	2.38	17.0	83.2
4	0.80	5.7	88.9
5	0.73	5.2	94.2
6	0.39	2.8	95.9
7	0.25	1.8	98.7
8	0.18	1.3	100.0

Table 5. Communalities (range 0.0–1.0) of 7 wing characters as determined by principal components analysis. Characters with lower communalities should partition the OTU’s (populations) into more meaningful groups, i.e., they are most diagnostic.

Character	Communality
1) FWLE	0.94540
9) HWLW	0.91284
3) FWLW	0.75851
6) FDLW	0.73140
14) SUHW	0.68258
10) HDCL	0.61904
15) USGC	0.54793
13) DISC	0.21685

ordered color (DISC and USGC) and silver-spotting (SUHW) characters provide a more reliable means to discern groupings of OTU’s. Figure 11 graphically represents the characters in relation to the second and third principal components.

The communalities (Table 5) indicate that most of the size characters are highly intercorrelated, i.e., in total they explain most of the observed variability. This is not surprising as 5 of the characters were continuous and displayed a wide range of variation. In contrast, characters DISC, USGC and SUHW have relatively low communalities, i.e., when combined with the other 5 characters, they explain a lesser proportion of the observed variance in the wing characters. As these only poorly correlate with any size characters, the PCA demonstrates that the three non-parametric characters, DISC, USGC and SUHW, are best at distinguishing the groups of OTU’s. These results may be somewhat biased due to the non-parametric nature of qualitative characters. Nonetheless, other numerical taxonomic techniques confirm that characters DISC, USGC and SUHW can best partition the OTU’s (Arnold, 1983, 1985).

Factor loadings of the first three principal components of each OTU were used to compute factor score for the 35 OTU’s. Figure 12 depicts interrelationships of OTU’s in the first three principal components and represents 83.2% of the variance in the original data matrix. The remaining 17% of the variance might modify positions of the OTU’s as they are depicted in Figure 12. Based primarily on size characteristics, all green morphs (OTU’s #22, 29–35) cluster together near the center of the plot. However, several morphs from the North Coast Range (OTU’s #12, 14), South Coast Range (#2), Sierra Nevada (#16, 17) and Tehachapi Mountains (#23, 24, 26, 27) also lie in the same general area. Only the 3 *S. callippe juba* OTU’s and the *S. callippe laura* OTU’s (#18, 19, 20, 21) form a discrete cluster. *S. callippe callippe*, *S. c. comstocki*, and *S. c. liliana* OTU’s (#1–12) are bisected by the cluster of green-morph OTU’s. Thus the principal components analysis corroborates the finding of the discriminant function analysis that overall size is a useless character for distinguishing subspecies of *Speyeria callippe*. Qualitative characters such as DISC, USGC, and SUHW can better partition individuals into populations than size characteristics.

DISCUSSION

The description and explanation of variational patterns may be examined one character at a time or with many characters simultaneously. The trend in geo-

graphic variation studies has been from univariate and bivariate analyses to multivariate analyses (Gould and Johnston, 1972). Multivariate studies reveal not just correlations between characters, but correlations among suites of characters within the sampled populations.

My univariate and multivariate analyses of geographic variation, indicate that many of the characters previously used to distinguish subspecies of *S. callippe* are useless as taxonomic characters. This study, one on phenetic variation in non-ordered state characters (Arnold, 1983), and another on the relationship of geographic variation in morphological and climatic variables (Arnold, 1985), demonstrate that most of the previously recognized subspecies of *callippe* are invalid based on the currently used characters. If subsets of OTU's derived via the univariate analysis are homogeneous for the characters in question, and there is a pattern to the variation, it should belong to geographically contiguous regions (Sneath and Sokal, 1973). Those sets of localities that are statistically homogeneous and geographically contiguous can be categorized as being biologically homogeneous and recognized taxonomically as subspecies. The univariate analysis demonstrates that the variation in 7 of the 8 characters is discordant. The pattern of variation in only one character, ventral disc color (DISC), correlates with geography and can be used as a basis for delimiting subspecies. Similarly, the multivariate techniques corroborate that DISC is the best character for partitioning populations, while the 5 continuous characters vary discordantly and the OTU's cannot be effectively grouped. DISC, USGC, and SUHW exhibit less variability, and thus can more effectively partition the populations. One advantage of PCA is that the relationships between the OTU's can be viewed without prior clustering, in this study, the grouping of populations into subspecies. Another important feature is that the trends in variability can be related to the actual characters which cause them (Moulton, 1973).

PCA has been used successfully in examining populations for phenetic intermediacy (Rising, 1968, 1970); however, since the technique does not maximize differences between biologically meaningful reference samples, it is not as powerful a tool for studies of hybrid or blend zones, or zones of abrupt phenetic transition as is discriminant analysis (Rohwer, 1972). Indeed, the discriminant analysis indicated that the previously recognized 16 subspecies were so poorly defined that only 43.2% of the individuals of unknown subspecific identity could be correctly identified based upon the same characters other lepidopterists have used to distinguish these "subspecies."

One of the major objections expressed by the opponents of the subspecies is that the trinomial system forces biologists to make arbitrary decisions that frequently distort the real nature of character variation and bias subsequent analysis (Hagmeier, 1958; Wilson and Brown, 1953). Also, most of the thorough studies of geographic variation show that independent characters vary discordantly in space (Gillham, 1956), in time (Doutt, 1955; Packard, 1967; Mason, 1964), and that single-character variation tends to be clinal (Sibley, 1954). As the environment exerts differing selective forces on differing characters one should expect that discordant variation will occur more frequently than concordant variation. The phenotypes thus assembled under the name of a subspecies might be so heterogeneous that the subspecies concept loses nearly all meaning. Often the only practical way to identify subspecies, such as those recognized by many butterfly

taxonomists, is by geographic location. Yet this may obscure the true patterns of geographic variation in a species.

Statistical analyses of geographic variation have advantages over more subjective methods. They are repeatable, knowledge obtained subsequently can be incorporated, and are objective to the extent that they attempt to describe variation before partitioning into subspecies. A thorough character analysis can demonstrate that discontinuities are correlated with disjunct distributions or with abrupt changes in the environment. These qualities are all too often absent in systematic procedure at the infraspecific level.

Many subspecies have been based on too few characters, poorly chosen characters, or inadequate analysis of geographic variation of characters (Wilson and Brown, 1953). Diagnostic markings and other slight external characters of necessity serve as prime criteria for distinguishing museum specimens. Nevertheless, the objective of many describers of subspecies is to discern minute typological differences in samples of populations from different localities rather than to study the similarity of samples or variability within a population (Burt, 1954; Hubbell, 1954). The mere pigeonholing of populations at infraspecific levels, especially when the range of variation has not been ascertained for several characters, conveys a false impression of uniformity (Bogert, 1954). Subspecific names should be employed to designate recognizably different assemblages of populations within a species (Mayr, 1969).

REVISION OF THE SUBSPECIFIC TAXA OF *SPEYERIA CALLIPPE*

Results of the several numerical taxonomic techniques employed in this study and others (Arnold, 1983, 1985), provide a basis for making taxonomic decisions at the infraspecific level. The 16 currently recognized subspecies of *Speyeria callippe* are reduced to 3 taxa: *callippe callippe* (Bdv.), *callippe nevadensis* (Edwards), and *callippe semivirida* (McDunnough).

Ventral disc color (DISC) is the best character for distinguishing the 3 subspecies. All populations with brown ventral discs, no matter what shade of brown, should be referred to as *S. callippe callippe*. These include silvered and unsilvered populations and those with several shades of brown scaling varying from reddish-brown to chocolate brown in color, and ranging from the Mt. Shasta–Trinity Alps region to San Diego, California.

Populations from southeastern Oregon, with greenish-brown or brownish-green ventral discs are grouped as *S. callippe semivirida*. All green disced populations from the east slope of the Sierra Nevada Mtns. and Great Basin are grouped as *S. callippe nevadensis*.

Most characters previously used are too variable to diagnose subspecies. These include general size, silver-spot pattern, spot color, dorsal melanization, dorsal ground color, and ventral margin banding characters (Arnold 1983, 1985). The revised taxonomy is as follows:

callippe callippe (Bdv.), 1852

c. comstocki (Gunder), 1925 New Synonym.

c. liliانا (H. Edwards), “1876” (1877) New Synonym.

c. elaine dos Passos and Grey, 1945 New Synonym.

c. rupestris (Behr), 1863 New Synonym.

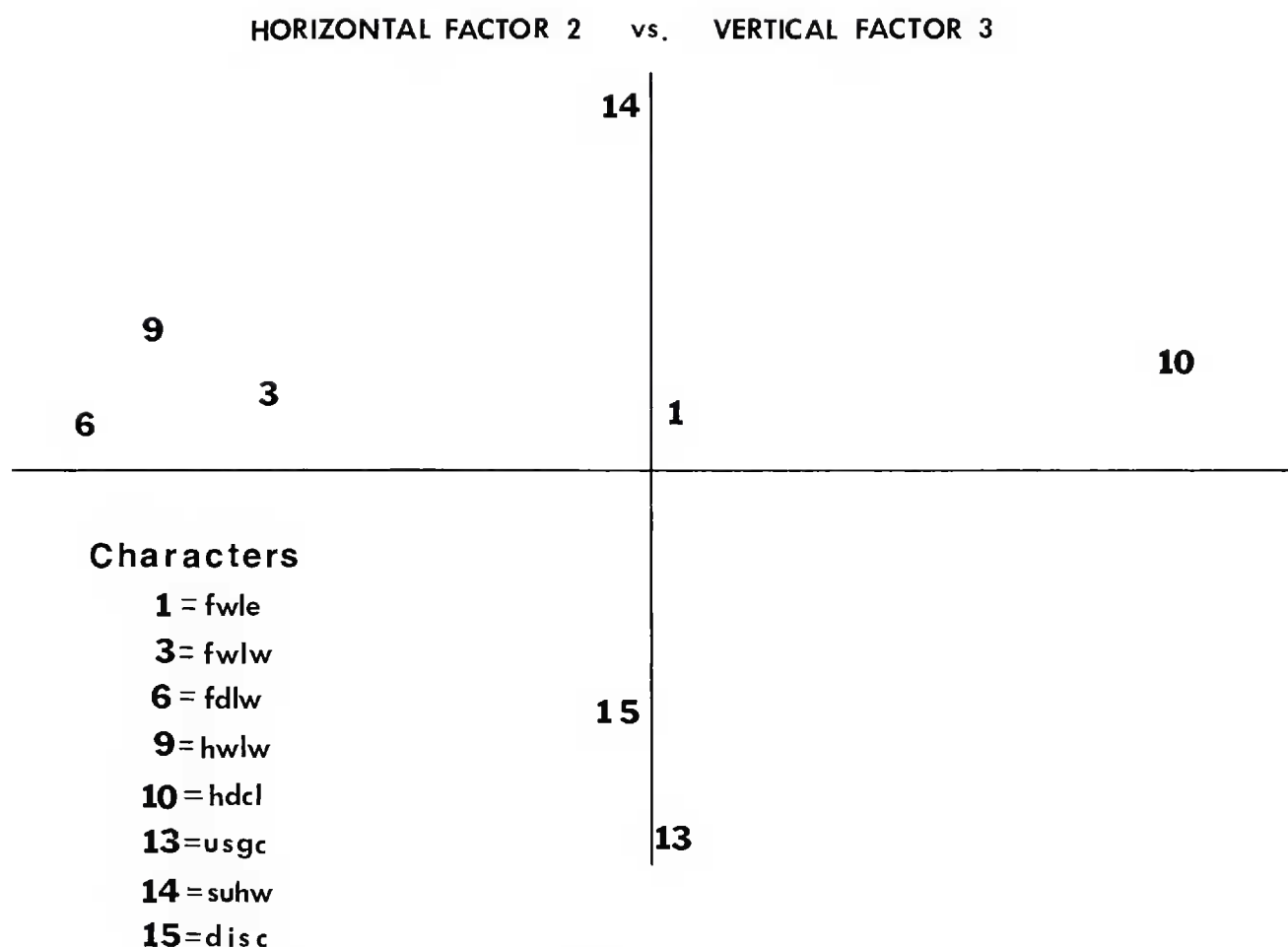


Figure 11. Graphic representation of principal components numbers 2 and 3 based upon characters FWLE, FWLW, FDLW, HWLW, HDCL, USGC, SUHW, and DISC. The underlying cause of horizontal factor number 2 is attributed to overall size, whereas vertical factor number 3 is largely due to wing coloration characters.

- c. juba* (Bdv.), 1869 New Synonym.
- c. laura* (Edwards), 1879 New Synonym.
- c. sierra* dos Passos and Grey, 1945 New Synonym.
- c. macaria* (Edwards), 1877 New Synonym.
- c. laurina* (Wright), 1905 New Synonym.
- callippe nevadensis* (Edwards), "1870-71" (1870)
- c. harmonia* dos Passos and Grey, 1945 New Synonym.
- c. meadii* (Edwards), "1872-73" (1872) New Synonym.
- c. gallatini* (McDunnough), 1929 New Synonym.
- c. calgariana* (McDunnough), 1924 New Synonym.
- callippe semivirida* (McDunnough), 1924.

IMPLICATIONS FOR CONSERVATION

The San Bruno Mountain (San Mateo County, California) population of *Speyeria callippe callippe* was proposed for recognition as an Endangered Species by the U.S. Fish and Wildlife Service in 1978. Although the butterfly is no longer known from its type locality, San Francisco, Howe (1975) believed that the name *Speyeria callippe callippe* applied to the population at nearby San Bruno Mountain. Housing developments threaten to destroy a significant portion of the butterfly's habitat at this site. In 1978, the Endangered Species Act of 1973 could legally recognize invertebrates as Endangered Species at the population, subspecies, or species level. However, the Tellico Dam-Snail Darter controversy resulted

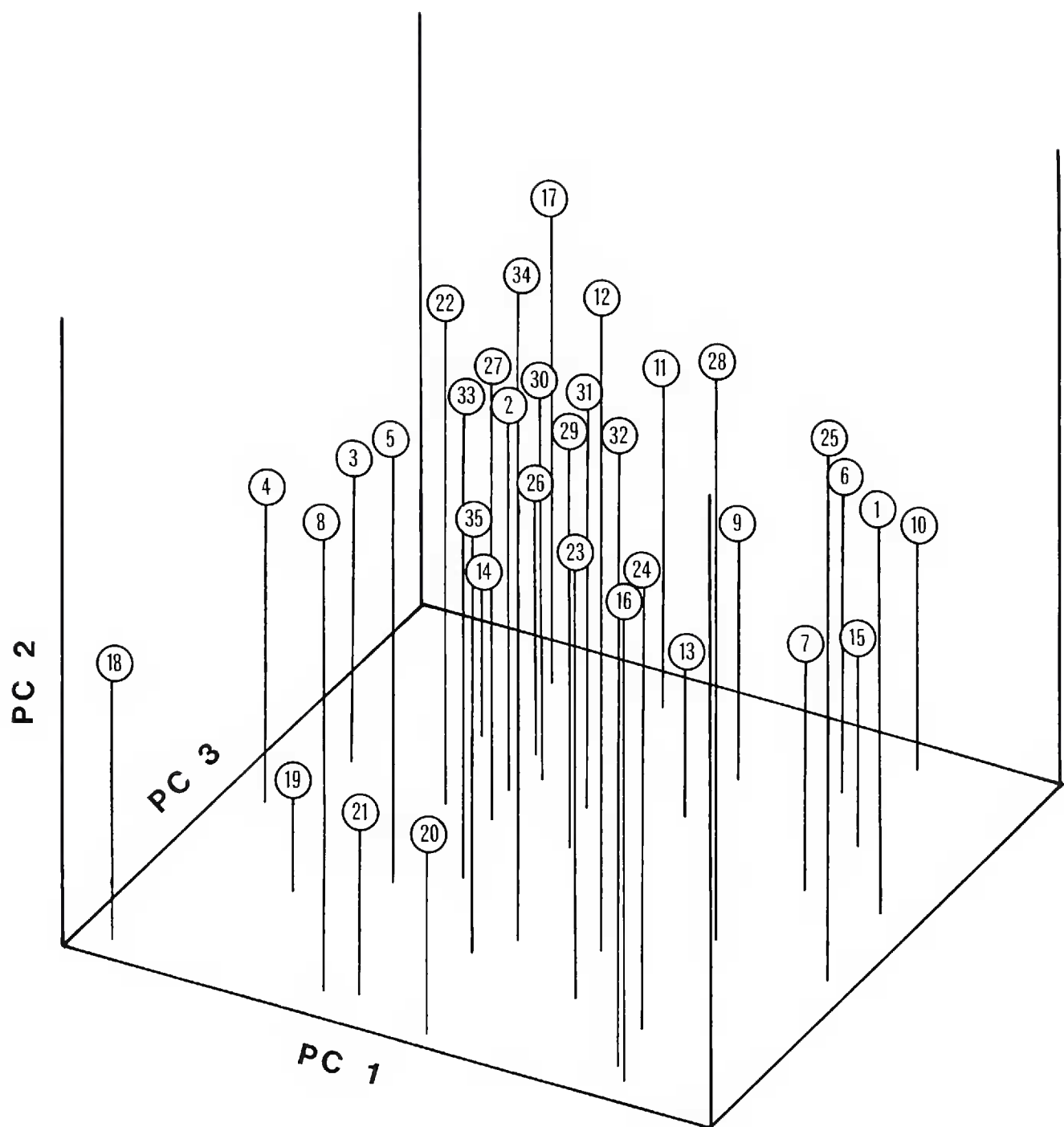


Figure 12. Three-dimensional plot of 35 *Speyeria callippe* populations based on the first three principal components. Labels PC 1, PC 2, and PC 3 on the axes refer to the first three principal components. Populations are coded as in Table 1.

in several amendments to the Endangered Species Act, including nomination of only formally named taxa, i.e., unnamed invertebrate populations could no longer be proposed for protection. Considerable ecological study of San Bruno Mountain *S. callippe* has been conducted since 1976 (Arnold, 1981; Reid and Arnold, unpubl. data). Although this population of *S. callippe* is no longer considered a distinct subspecies whose range is restricted to only San Bruno Mountain, it may represent a unique ecotype, similar to the situation recently elucidated by Murphy and Ehrlich (1980) for *Euphydryas editha* (Bdv.) in the San Francisco Bay Area. However, comparable ecological studies of other Bay Area *S. callippe* populations have not been completed.

SUMMARY

Univariate and multivariate statistical analyses of geographic variation in 8 wing characters of *Speyeria callippe* revealed that only one character, ventral disc

color (DISC), can partition populations into meaningful groups. Other size and color characters used to differentiate previously recognized subspecies do not correlate with geography. These analyses provide a basis for revision of the subspecific taxonomy of *S. callippe*. The 16 previously recognized subspecies are reduced to three, whose morphology correlates with geography.

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